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CONTRIBUTIONS TO THE LIFE HISTORY OF WIDDRINGTONIA CUPRESSOIDES

W. T. SAXTON

(WITH PLATES I–III AND THREE FIGURES)

In a previous communication (**10**) the writer has pointed out certain peculiarities in this genus, and in the genus *Callitris*, which mark them off sharply from all other Cupressineae which have been investigated. Many phases of the life history have now been fully investigated in both genera, and in the main confirm the results previously published, although certain points require modification or correction. The investigation of both genera has been carried on simultaneously, the original intention having been to present the results in one paper; it has however been found that the differences between the two are more radical than was anticipated, and the present communication relates solely to *Widdringtonia*. A similar account of *Callitris* will be published very shortly (**11**), in which the results of both investigations will be discussed. The methods used have not differed materially from those previously employed.

1. The male cone

The sporophylls are arranged, like the leaves, in decussate pairs. Each sporophyll is peltate and bears four microsporangia[1] on the proximal side of its stalk. The output of spores from a sporangium is about 500. The structure of the sporophyll in a transverse section through the insertion of the sporangia is shown in fig. 1. The structure of the cone in radial longitudinal sections has already been figured (**10,** fig. 2). The anatomy of the sporophyll agrees exactly with that of *Callitris* and will be later described in that genus.

2. The female cone and the ovule

The young female cone consists of two spreading decussate pairs of sporophylls, each scale bearing seven or eight ovules on the proximal half of the upper surface, and close to the median ridge.[2] Each megasporophyll is traversed by a large number of vascular strands and resin canals; near the top of the sporophyll the latter are evenly disposed all round the periphery, and inside each canal is a vascular bundle with the phloem on the side nearest the canal. On the lower (outer) surface of each scale is a small umbo.

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[1] MASTERS (**6**) says 2–3.

[2] In *W. Schwarzii* only three ovules are borne on each scale.

The structure of the ovule before and shortly after pollination has already been described and figured[3] (**10,** figs. 1 and 3). The ingrowth of the micropyle-closing cells is not followed by septation in them, as it is for example in *Pinus*. A transverse section of the micropyle is shown in fig. 2, in which it may be seen that the opening is often not entirely closed by the ingrowth of these cells. This figure shows a most remarkable resemblance to a similar section of the micropyle of *Bennettites*, figured by LIGNIER (**6,** fig. 31), as pointed out to me by Professor SEWARD.

Some time after pollination the sporogenous tissue becomes evident. Seen in median section it appears as about 18 or 19 large cells with dense cytoplasm and large lightly staining nuclei, sharply marked off from the surrounding cells, which have vacuolate cytoplasm and smaller deeply staining nuclei. The position and structure of these cells are indicated in figs. 3 and 4. Their number[4] is about 64, possibly exactly that number, in which case they are not improbably formed by repeated simultaneous divisions of a single archesporial cell. It is however quite as likely that the number is somewhat less than 64, and that they have not a common origin from a single archesporial cell. They are all exactly alike when first differentiated, and their subsequent behavior indicates that they are spore mother cells, only one of which, however, is functional. Sometimes a single layer of tapetal cells may be seen a little later.

At a somewhat later stage, one of the central mother cells becomes a very little larger than the remainder, the nucleus also enlarges very slightly, and the wall becomes a trifle thicker than that of its neighbors. This is the functional megaspore mother cell. At about the same time the non-functional cells elongate somewhat, and certain peculiar structures make their appearance at or near their ends. These structures appear as homogeneous dark brown bodies of various shapes, and may be conveniently called the "brown bodies" (fig. 5). That they are not produced artificially is clearly indicated by the fact that they are found only in the sporogenous tissue, and at first only in a very definite position at the two poles of the cells. Later they may be somewhat displaced from this position.

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[3] The wings of the ovule were accidentally described (p. 166) as being only one cell thick. This is never the case, even close to the margin.

[4] Calculated on the assumption that the actual number is to the number seen in median section as $\frac{4}{3}\pi r^3$ to πr^2.

The only structures previously recorded as occurring in megaspore mother cells, with which the "brown bodies" might conceivably be correlated, are the "kinoplasmic centers" found in *Ginkgo* (CAROTHERS **1**) and other gymnosperms. It seems unlikely, however, that the "brown bodies" are of this nature, especially as their existence has not been proved in functional mother cells. They seem to be entirely unstained by Delafield's hematoxylin, and show a marked resemblance in this respect, as well as in color and consistency, to certain nucleoli, although nucleoli usually stain deeply with this reagent. At about this time some of the cells in or near the central axis of the nucellus begin to break down or to elongate, no doubt in preparation for the rapid growth of the pollen tube and embryo sac (fig. 6).

3. Megasporogenesis

About a week after the events described have taken place the functional megaspore mother cell is found in synapsis (figs. 7 and 9), the surrounding cells retaining more or less their former character. No preparation has been obtained which shows either of the reducing divisions. Figs. 10 and 11 show a state of things rather difficult to interpret. The arrangement of the cells marked 1, 2, 3 in fig. 10, and the character of the nucleus of "1" as seen in fig. 11, at once suggest that "1" is the megaspore preparing for its first division, and that "2" and "3" are two sterile cells cut off in the heterotypic and homotypic divisions respectively. A comparison with figs. 12 and 13, which unquestionably represent two normal megaspores before the first division, indicates however that either this interpretation is not the true one or that the ovule was not normal.

In the preliminary account (**10**) a stage was figured which seemed to indicate a very large number of megaspores. Although every preparation of the same age showed an almost identical structure, it has proved to be merely that characteristic of an ovule which is destined to be abortive.

It is uncertain whether three or four potential megaspores are formed, but it is quite certain that only one becomes functional. As shown in fig. 12, the surrounding cells begin to disintegrate so quickly that the other cells derived from the functional mother cell cannot be recognized. There is some indication that it is not the lowest megaspore which develops, as is usually the case, but no definite statement can be made. The wall of the mature megaspore is so thin that it can be distinguished only with great difficulty.

In fig. 13 a cell immediately above the megaspore shows one of the "brown bodies" very distinctly, and a part of this cell is drawn on a larger scale in fig. 14. Fig. 13 indicates that polarity may be established in the embryo sac before the first division of the megaspore nucleus, and many other preparations show the same, but by no means all (compare figs. 12 and 15).

4. The female gametophyte[5]

After the first division of the megaspore nucleus, the walls of the embryo sac and disintegrating mother cells can scarcely be distinguished. Their thickness has been unavoidably exaggerated in fig. 15. In the preparation figured (the only one showing a binucleate sac), no polarity is evident, nor are the nuclei arranged quite parietally. After the next division, however, the four nuclei are imbedded in (or rather protrude inward from) a very thin parietal layer of cytoplasm, and there is some indication of polarity, two nuclei being situated near the upper end and two near the lower end of the sac, the two pairs being symmetrically placed with regard to one another (fig. 16). This is distinctly interesting in view of the recently revived opinion that the embryo sac of angiosperms is derived from that of gymnosperms by a series of reductions, although it is to be noticed that certain "primitive" angiosperms do not show the polarity so characteristic of the vast majority. The growth of the embryo sac (prothallus) proceeds rapidly now toward the apex of the nucellus,

[5] As pointed out by COULTER and CHAMBERLAIN (2), the history of a gametophyte should start from the mother cell rather than from the spore, but practically it is more convenient to consider sporogenesis separately.

the apical part becoming very narrow and closely resembling the tip of an advancing pollen tube. The breaking down of certain cells in the axis of the nucellus, facilitating the upward growth of the prothallus, has already been referred to. The divisions of the nuclei are doubtless simultaneous until at least 64 are present (exactly that number having been counted in serial sections), and possibly until wall formation begins. Fig. 17 shows in outline the general structure of the nucellus at the time when 64 nuclei line the embryo sac. Fig. 18 is part of a tangential section of the prothallus after free nuclear divisions have ceased. The nuclei each contain a single nucleolus which can invariably be seen to be hollow.

Cell formation takes places as in most other gymnosperms, and has already been described and figured (**10,** fig. 9). A large number of nuclear divisions have been seen in the "alveoli," certain features of which strongly recall the peculiar divisions described by LAWSON (4) as occurring at this time in *Cryptomeria*. All the earlier phases (figs. 19 and 20) are quickly passed through, but that shown in fig. 21 is very persistent, the marginal fibers having almost the appearance of a cell wall. The wall between the nuclei, however, is always developed, but in cases where its width does not nearly equal the diameter of the cell, it is just possible that wall and fibers may disappear again and thus give rise to a binucleate cell. It has not been demonstrated, however, that binucleate cells ever originate in this way, and the chief interest of fig. 23 is in providing a connecting link between the very peculiar divisions giving rise to the temporarily binucleate cells of *Cryptomeria* and the ordinary mitotic divisions in normal conifer prothalli.

Very soon after cell divisions are complete, the archegonium initials make their appearance. These become considerably larger than the surrounding cells and their nuclei are a little larger (fig. 22). The position of the archegonia is somewhat variable, but usually two distinct types seem to be formed: (1) a single group of about ten or more, directly abutting on the swollen end of the pollen tube;[6] (2) one, or usually more than one, group of few or several archegonia (rarely a single archegonium) which are found near, but not abutting on, the upper part of the pollen tube, and deep-seated in the prothallus (fig. 23). It is certain that neck cells are formed in the former (1), although they are very evanescent and much more difficult to demonstrate than in the archegonia of *Pinus*, for example; but they have not been demonstrated in the deep-seated archegonia (2), although it is not unlikely that this is merely due to the difficulty of differentiating them from other cells of the prothallus. In a recently published account of *Juniperus* (OTTLEY **9**), a case is described and figured in which a small deep-seated archegonium occurred outside the normal group. The figure leads one to suppose that no neck cell could be demonstrated, but no statement on this point is made in the text. After fertilization no neck cells can be found in either type of archegonium, which accounts for the suggestion made in my former paper (**10**) that neck cells are never formed in *Widdringtonia*. The neck, where present, consists of a single tier of four cells (fig. 23).

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[6] In the few cases where two pollen tubes reach maturity, a group of this kind is organized in connection with each tube.

The central nucleus of the archegonium divides (in the first type of archegonium) simultaneously in the whole group (fig. 24), a conspicuous spindle being organized with long, slender, and considerably twisted chromosomes (fig. 24). The reduced number of chromosomes (six) may be counted fairly readily in this division. It is to be noticed in fig. 23 that although the central nucleus of every archegonium in the basal group is dividing, yet the nuclei of the other archegonia are still in the resting condition. The evidence that these do not divide is purely negative, but the possibility of the deep-seated archegonia being really archegonium initials only, must not be overlooked. The case shown in fig. 16 of my former paper (**10**) indicated that rarely a persistent ventral canal nucleus is formed, but out of scores of prothalli examined, containing thousands of archegonia, this is the only case in which such a state of things was clearly indicated. In no other preparation has the ventral canal nucleus been certainly identified, although the occurrence of the spindle which initiates its formation furnishes additional evidence that it must be formed. Doubtless it is normally very evanescent. From STRASBURGER'S (**12**) figures of the same nucleus in *Juniperus*, it would seem that it is by no means a conspicuous object in that genus, and although LAWSON (**5**) figures a large ventral canal nucleus in *Thuja*, it evidently disappears quickly, as it is not figured in the mature archegonium, and the same was found in OTTLEY'S recent paper on *Juniperus* (**9**).

The formation of binucleate and multinucleate prothallus cells has already been described. It is initiated at about this time, but nuclear divisions continue to occur during the earlier phases of embryo formation. Two such dividing nuclei are drawn in figs. 26 and 27.

The structure of the mature archegonium is much like that of other Cupressineae, with a large, centrally situated oosphere nucleus and a basal (or sometimes partly lateral) vacuole (fig. 28). The neck cells do not persist long, the archegonia of the basal group finally opening into the pollen tube.

The total number of archegonia of both kinds organized in a prothallus varies considerably. Sometimes there are only about 25–30, usually about 40–70, and occasionally as many as 100. The microphotograph (text fig. 1) is taken from a tangential section of a prothallus in which about 100 archegonia were present. About 50 of these appear, cut transversely, in this section. A prothallus containing about 50 in all was sketched in my preliminary paper (**10,** fig. 15).

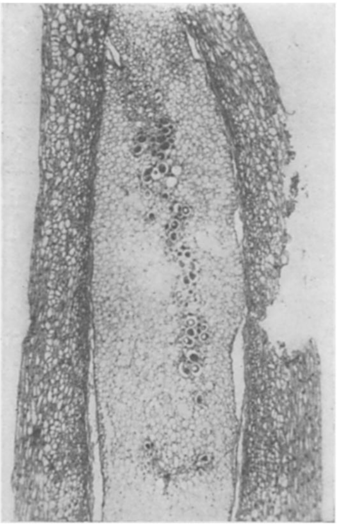

FIG. 1.—Microphotograph of a tangential section of a prothallus in which about 100 archegonia were present.

5. The male gametophyte

The earliest stages of the germination of the microspore have been already described, but the description will be briefly repeated here. The mature pollen grain is uninucleate and there is no evidence that any prothallial cells are formed. Thus the "pollen grain" is here synonymous with the "microspore." The earliest stage of germination usually consists in the formation of a solid outgrowth from the exospore, which applies itself closely to the surface of the nucellus, sometimes with a tendency to grow down between the nucellus and integument. About three pollen grains usually begin to germinate in each ovule, but generally only one and never more than two reach maturity. A little later the solid outgrowth of the exine becomes hollow, and the intine then grows through it, forming the tube, which at once penetrates a short way into the nucellus, the single nucleus passing into the tube. Occasionally a tube is formed at once on germination.

The time during which the pollen tube remains uninucleate seems to vary a good deal, a tube with a single nucleus having been found associated with a four-nucleate prothallus (fig. 29), while in two or three cases a tube containing three nuclei was found in an ovule before the first division of the megaspore nucleus; one such case is shown in figs. 30 and 31. No differentiation of cytoplasm can be seen here around the upper nucleus, doubtless the body cell nucleus, but the preparation is noteworthy as the only one in which a difference in size could clearly be seen between the two sterile nuclei, that nearest the apex of the tube (the "tube" nucleus) being considerably larger. Fig. 32 is a detailed drawing of the tube, the position of which is shown in fig. 17. Its size is approximately the same as that of figs. 30 and 31, but the structure is somewhat different. The two sterile nuclei are precisely alike in every respect, as they are in every preparation in which they occur, except in the one noted above and in one abnormal tube referred to later. The body cell is here sharply demarkated from the surrounding cytoplasm in which the other nuclei are imbedded.

It should be mentioned here that the occurrence of only two nuclei in the tube at a stage somewhat later than this, as previously reported (**10**), has not been confirmed in any other preparations. It is curious that, in fact, the binucleate stage has never been certainly identified, as it is not improbable that the case just mentioned is really a three-nucleate tube, and that defective preparation is responsible for the appearance of only two. It may be added that the preparation there figured is from material collected very soon after the work was begun, and before the best fixing agents and oven periods had been satisfactorily ascertained. On the other hand, it may be that the uninucleate condition had persisted later than usual in this case, and that only two nuclei are actually present. In any event, it is certain that the two sterile nuclei must be cut off in somewhat rapid succession.

After they are formed, the pollen tube renews its activity and rapidly grows until it reaches the megaspore membrane. It is only rarely that the apex of the membrane is penetrated; more commonly the tube grows down a little farther before entering the prothallus. The entry is however almost invariably effected before the commencement of wall formation, the latter usually taking place only after the tube has taken up its final position. At the point where the pollen tube pierces the megaspore membrane, a slight constriction almost invariably occurs, while the tip of the tube dilates a little to form a kind of vesicle just within the prothallus. Preparations are often met with in which the contents of the tube are just opposite the constriction, indicating a certain amount of difficulty in passing this point. Inside the prothallus the wall of the tube becomes thicker (fig. 33). When the difficulty of passing this point is overcome, the tip of the tube rapidly advances to about, or a little beyond, the middle of the prothallus. During the whole later growth of the tube the individuality of the body cell is less evident than at the stage shown in fig. 32, and its cytoplasm may be quite indistinguishable from the rest of the tube cytoplasm. A case of this kind, in which all three nuclei are imbedded in a common mass of cytoplasm, has already been figured (**10,** fig. 10), and is not uncommonly met with (see also fig. 33).

Perhaps the most usual case is shown in figs. 34 and 35. Here the body cell is distinct, not only from the surrounding cytoplasm of the tube, but also from the cytoplasm in which the sterile nuclei are imbedded. With the triple stain, the cytoplasm of the body cell stains red, that in which the sterile nuclei are situated takes the orange, while the rest of the tube cytoplasm is a deep violet. In later stages the body cell increases very considerably in size. Its structure shortly before division has already been described and figured. Some uncertainty was expressed as to the fate of the two sterile nuclei. It was suggested that they were probably absorbed by and became indistinguishable from the cytoplasm. Later preparations have in the main supported this view, but sometimes these nuclei are recognizable in connection with a quite mature body cell, in a prothallus in which wall formation is complete.

Only a single preparation has been obtained showing the two male cells fully organized (figs. 36 and 37). Each cell is surrounded by a definite wall (or membrane) and is more or less hemispherical. The cytoplasm is dense and very homogeneous, and in the center of each cell is a large nucleus with no nucleoli. The entire absence of starch in the male cells is noteworthy, as compared with other Cupressineae. In this preparation the two cells are just beginning to separate, and probably they would finally become rounded off as reported by LAWSON (4) in *Libocedrus*. In contact with one of these cells (see figs. 36 and 37) is a curious body which presents the appearance of a vesicle containing a number of small, deeply stained granules. No light can be thrown on the morphology or functions of this body. No trace whatever can be seen of the two sterile cells. Possibly their disappearance may be connected with the appearance of the vesicle, but this is merely conjecture.

6. Fertilization and embryogeny

The actual process of fertilization has not been seen in *Widdringtonia;* probably it agrees essentially with that in other Cupressineae as has been found to be the case in *Callitris*.

The first stage of the proembryo shows two free nuclei arranged lengthwise in the archegonium (fig. 38). The two nuclei are alike in size and structure. No starch is noticeable in the proembryo at this stage, but in all later stages seen, a considerable amount of starch is present. In later stages the structure has often been very difficult to interpret. Although a considerable number of preparations has been obtained, the sections have nearly always happened to be oblique. In two cases the following method has been successfully employed in order to get over this difficulty. Serial sections were drawn in ink on gelatin plates, the drawings being then placed together in sequence. If the thickness of the plates is to the thickness of the sections as the diameter of the drawing is to the diameter of the section, then a solid figure is obtained which represents accurately the object sectioned, the structure of which can be seen fairly clearly through the transparent gelatin. The gelatin plates can be easily stuck together by wetting them slightly.

Figs. 39 and 40 are reconstructed from serial sections. They show proembryos containing five and ten nuclei respectively. In fig. 39 delicate walls can already be seen between the nuclei, the appearance of which indicates that they probably arose as cleavage planes. In fig. 41 a transverse section of the upper four nuclei is shown. The presence of kinoplasmic radiations (spindle fibers?) between these four nuclei indicates that probably they had a common origin and that after the first division of the oospore the basal nucleus remains undivided. It is evident that the early development of the proembryo does not show any resemblance whatever (after the first division) to that described by LAWSON (**5**) for other Cupressineae (*Thuja* and *Libocedrus*), and by OTTLEY (**9**) for *Juniperus*, where eight free nuclei are organized before walls are laid down.

Fig. 40 shows diagrammatically the structure of a ten-nucleate proembryo entirely filling the archegonium. It was not quite clear whether the walls extended to the upper three nuclei or not. The stages between figs. 39 and 40 are missing, and it is difficult to guess how the second form arose from the first. Probably there is some variation in the earlier divisions; compare, for instance, fig. 40 with the two proembryos figured in my preliminary account (**10**, fig. 16). Embryo development has already been briefly described.

Fig. 42 is a drawing of a germinating seed before the cotyledons are withdrawn from the testa. Fig. 43 shows the upper part of the same seedling after removal of the testa. Often the testa is carried up on the tip of one of the cotyledons in germination. The seedling structure (anatomy) of *Widdringtonia cupressoides* differs somewhat from that recently described by HILL and DE FRAINE for other species (**3**), and an account of it has already been published from this laboratory, together with a description of a remarkable twin seedling of the same species (MORRIS **8**).

In the plumular development a pair of opposite leaves succeeds the cotyledons, and is found in a plane perpendicular to that of the cotyledons. These leaves are followed by from about three to about ten alternating whorls of four leaves (text fig. 2). The structure and leaf arrangement of a tricotyledonous embryo have proved rather interesting. The three cotyledons are equal in size and have probably been equivalent in development and are succeeded by alternating whorls of three primordial leaves. This is shown in the photograph (text fig. 3). The transition region is longer than in the normal seedling, and only at its lower end is there any indication that the three cotyledons are not all equivalent. Here two of the xylem groups grow somewhat smaller and approximate and finally join, thus giving the diarch root structure typical of the normal seedling.

7. Abnormalities

The tip of the pollen tube of fig. 23 contains a curious body cell which is shown more highly magnified in fig. 23*a*. Its appearance strongly suggests that it is not a normal body cell just after the division of the nucleus, but that during or immediately following the division disintegration of the nucleus has begun.

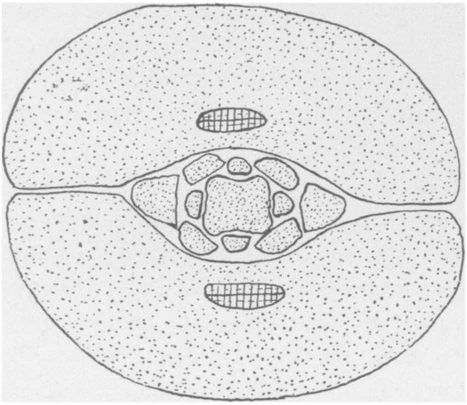

FIG. 2.—Diagrammatic cross-section of the cotyledons and plumule of *Widdringtonia*, showing arrangement of the primordial leaves in a dicotyledonous seedling.

In fig. 34 a slight irregularity is evident, inasmuch as a small fragment of the body cell nucleus has been constricted off and left just behind in the cytoplasm of the cell. It is barely possible that this may have been caused by defective preparation, but one other case has been seen in which a small papilla protruded in precisely the same direction from the body cell nucleus (not figured). Moreover, no such phenomenon has ever been seen by the writer in the case of any other large nuclei, either in *Widdringtonia* or any other plant.

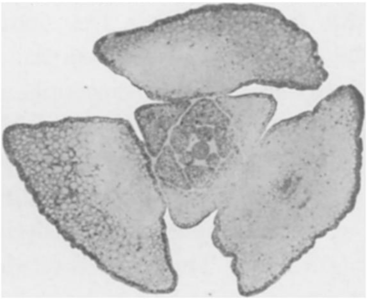

FIG. 3.—Photograph of a transverse section of a tricotyledonous seedling.

One very curious abnormal male gametophyte is shown in fig. 44. Here the sterile nuclei are in the swollen tip of the tube (which is surrounded by the usual group of archegonia), but the body cell has been left far behind. The nuclei are shown in more detail in figs. 44*a* and 44*b*. It is noticeable that the body cell does not exhibit such a distinctive structure as is normally the case, while one of the sterile nuclei is clearly larger than the other and is also distinguished structurally from it. This also is unusual and suggests the possibility that this larger cell might have eventually taken the place of the tardy body cell.

The other two cases figured which seem to be abnormal are both taken from archegonia occurring in prothalli in which the pollen tube had lost its contents, but in which no proembryo was evident. Both might conceivably be taken to represent stages in the fusion of sexual nuclei. Fig. 45 shows an archegonium which was unhesitatingly considered to contain the sexual nuclei in contact, but on examination of these nuclei with a more powerful objective they were found to have the structure indicated in fig. 45*a*. The whole of the contents seems to consist of homogeneous and rather dense nuclear plasm except for the four nucleoli (?). Each of these nucleoli (?) consists of a membrane from the inside of which a plasmic strand has contracted on which are regularly arranged about six (three or four in optical section) very deeply staining bodies, of the shape and size figured. It is suggestive that the number of these bodies in each nucleolus (?) should be the same as the haploid number of chromosomes. It is also suggestive that two of these nucleoli (?), differing only in size, should be present in each of the fusing nuclei, if such they are.

Figs. 46*a* and 46*b* are two successive sections of the same archegonium nucleus. The structure is so strikingly different in the two that it is difficult to believe they are actually parts of the same nucleus; but the fact is clear. In each section all the deeply staining structures (chromatin granules ? and nucleoli ?) have been figured, whether or not they occur in the same optical focus.

Beyond the suggestion made above, I have no opinion to offer on these figures. Since they occur at such an interesting stage of the life history it seems desirable to place them on record.

8. General

Since much variation has been noticed among the Cupressineae in the time elapsing between pollination and fertilization, it is interesting to compare *Widdringtonia* in this respect. The chief point of interest is that although a very long period intervenes between pollination and fertilization, yet there is no break in the continuity of development, such as probably occurs in those temperate conifers which are pollinated in one season and fertilized in the next. It is further interesting to notice that there are absolutely no fixed periods, so far as the writer can judge, when definite stages may be found. It may be not out of place to observe that these facts have made the working out of the life history very much more difficult than would otherwise have been the case, which must be the excuse for the gaps which still remain in the present account.

At the time of writing (November 1909), complete data are not available, but cones known to have been pollinated in January (or possibly early in February) of the present year are still far from ready for fertilization. They are still under observation and may probably be fertilized by the time this paper finally goes to press, in which case a postscript will be added.

Very young female cones may be found at any time, but soon die off unless pollinated. The time of appearance of the male cones is very variable. During the present year the writer has failed to find a single male cone, except in the early part of January. Nevertheless, recently pollinated ovules were collected at the end of June, so that there probably must have been male cones in the vicinity during May.

During 1908, male cones were collected in April and again in May (mature in both cases and separated by a full four weeks). A large number of trees were examined frequently and carefully during those months in 1909, without a single male cone being found. The following field notes of the different aged cones met with at one time and in one clump of trees may be of interest. About March 1 the following female cones were found: (1) very young; scales still widely open; pollinated (probably about one month previously); (2) medium size; still quite green; ovules with well-developed embryo sac; (3) full grown, brown, but with junction lines of scales still green; ovules with full-size embryo sac but no trace of cell formation; (4) full grown, uniformly light brown; integument discolored; young embryos; (5) dark brown, showing signs of dehiscence; mature seeds. It was afterward found that (3) could be segregated into two separate batches, in one of which fertilization took place about the end of April, in the other about the middle of September.

As stated in the introduction, it is not proposed to discuss the facts here reported until the corresponding facts in the life history of *Callitris* are published, when the two genera may conveniently be compared and contrasted.

Summary

The microsporophylls are arranged in decussate pairs and each bears four microsporangia.

The mature pollen grain is uninucleate.

The four equal megasporophylls are opposite and decussate.

About 64 megaspore mother cells are organized at the base of the nucellus, but only one is functional. Peculiar structures are noted at the poles of the non-functional megaspore mother cell.

The megaspore may show polarity before the first division of the nucleus, or when four nuclei are present. The divisions of the embryo sac nuclei are probably simultaneous.

Cell formation in the prothallus is normal in most respects, but certain peculiarities have been noted in the nuclear divisions which suggest comparison with *Cryptomeria.*

The archegonia are never situated at the apex of the prothallus, but in several groups organized in relation to the pollen tube and deep-seated in the prothallus. The lowest group abuts on the pollen tube; the upper groups do not, and may possibly represent archegonium initials. In the lowest group four neck cells are formed and a ventral canal nucleus is cut off. The total number of archegonia in a prothallus varies from about 30 to about 100.

The microspore nucleus remains undivided for a long time. In other respects the development of the male gametophyte is more or less normal, but the so-called "stalk" and "tube" nuclei are almost invariably exactly alike and tend to disappear completely in the mature pollen tube.

The proembryo completely fills the archegonium, but the arrangement of the cells is somewhat variable. Walls are formed when less than eight free nuclei are present.

The mature embryo has two (very rarely three) cotyledons.

The cells of the mature prothallus are all binucleate or multinucleate.

Stages in the life history are found not to correspond to definite seasons, and a long time elapses between pollination and fertilization.

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POSTSCRIPT (March 26, 1910).—Wall formation in the prothallus of ovules pollinated about January, 1909, is now taking place. Fertilization is likely to follow in the course of a few days. It may therefore be stated that an interval of fourteen or fifteen months will elapse, in this instance, between pollination and fertilization.

LITERATURE CITED[7]

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[7] A considerable number of papers bearing on the subject were quoted in my former paper. It is not necessary to repeat the titles here, only those actually cited in the text being given.

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EXPLANATION OF PLATES I–III

All figures were drawn with Zeiss camera lucida, microscope, and lenses, except figs. 39 and 40 (see text). In all: *b*, "brown bodies"; *c*, micropyle closing cells; *d*, megaspore mother cells; *e*, functional megaspore mother cell; *f*, male cells; *h*, integument; *n*, nucellus; *q*, body cell nucleus; *p*, prothallus; *r*, resin cavity; *s*, sterile nuclei; *t*, pollen tube; *v*, vascular bundle.

PLATE I

FIG. 1.—Transverse section of mature microsporophyll, showing positions of four microsporangia, resin cavity, and vascular bundle. ×35.

FIG. 2.—Transverse section through micropyle of an ovule about same age as fig. 3; the formation of the "wing" has only just begun. ×205.

FIG. 3.—Median longitudinal section of a young ovule, showing position of megaspore mother cells. ×85.

FIG. 4.—Section through megaspore mother cells in an ovule similar to fig. 3. ×480.

FIG. 5.—Two non-functional megaspore mother cells, showing characteristic appearance of the "brown bodies." ×825.

FIG. 6.—Part of nucellus of an ovule slightly older than fig. 3, showing formation of schizogenous cavities and sliding growth of three cells. ×205.

FIGS. 7, 9.—Megaspore mother cells in synapsis. ×825.

FIG. 8.—Position of mother cell of fig. 7 in relation to surrounding cells. ×205.

FIG. 10.—Sporogenous cells at a somewhat later stage (see text). ×500.

FIG. 11.—Cell 1 of fig. 10. ×825.

FIG. 12.—A functional megaspore and some of the surrounding cells. ×480.

FIG. 13.—A functional megaspore and one of the surrounding cells. ×480.

FIG. 14.—Part of upper cell in fig. 13, more highly magnified. ×1150.

FIG. 15.—A binucleate embryo sac showing disorganization of other sporogenous cells. ×360.

FIG. 16.—A four-nucleate embryo sac and the disorganizing mother cells surrounding it. ×205.

FIG. 17.—Longitudinal section of nucellus, showing position of pollen tube and embryo sac when 64 nuclei are present in the latter; the region occupied by disorganizing spore mother cells is shaded. ×35.

PLATE II

FIG. 18.—Some prothallus nuclei in tangential section of the sac, showing the hollow nucleoli. ×825.

FIGS. 19–21.—Three dividing nuclei in the "alveoli." ×1240.

FIG. 22.—Archegonium initial. ×205.

FIG. 23.—Part of a longitudinal section of a mature prothallus, showing the pollen tube, the basal group of archegonia, and three accessory archegonia; the nuclei of all the basal archegonia are dividing. ×120.

FIG. 23*a*.—The body cell of fig. 23. ×825.

FIG. 24.—Part of one of the archegonia of fig. 23, showing the spindle concerned in cutting off the ventral canal nucleus. ×825.

FIG. 25.—The neck of an archegonium in transverse section. ×205.

FIGS. 26, 27.—Dividing nuclei in the prothallus cells. ×1500.

FIG. 28.—Mature archegonium; the position of the pollen tube is indicated above the neck. ×360.

FIG. 29.—Young pollen tube; only a single nucleus is present. ×480.

FIG. 30.—Tip of young pollen tube showing three nuclei. ×825.

FIG. 31.—Part of nucellus, showing position of the tube of fig. 30. ×50.

Fig. 32.—Young pollen tube with body cell and two sterile nuclei; the position of this tube is shown in fig. 17. ×825.

PLATE III

FIG. 33.—Tip of pollen tube just entering the prothallus. ×205.

FIG. 34.—Tip of pollen tube after growth of the tube has ceased; the sterile nuclei with their surrounding cytoplasm form a distinct cell; a small fragment of the body cell nucleus has separated off. ×205.

FIG. 35.—The body cell nucleus of fig. 34. ×825.

FIG. 36.—Tip of mature pollen tube, showing position of male cells and the relation of archegonia to the pollen tube. ×205.

FIG. 37.—Male cells of fig. 36. ×480.

FIG. 38—Part of a transverse section of a prothallus, showing an archegonium containing two free nuclei, the daughter nuclei of the oospore. ×360.

FIG. 39.—Diagrammatic longitudinal section of proembryo with five nuclei; reconstructed from serial sections. ×170.

FIG. 40.—Similar section of proembryo with ten nuclei; reconstructed from serial sections. ×230.

FIG. 41.—One of the sections from which fig. 39 was constructed, slightly oblique, showing the upper four nuclei and the cleavage planes (?) between them. ×200.

FIG. 42.—Young seedling. ×1.5.

FIG. 43.—Cotyledons of same. ×3.7.

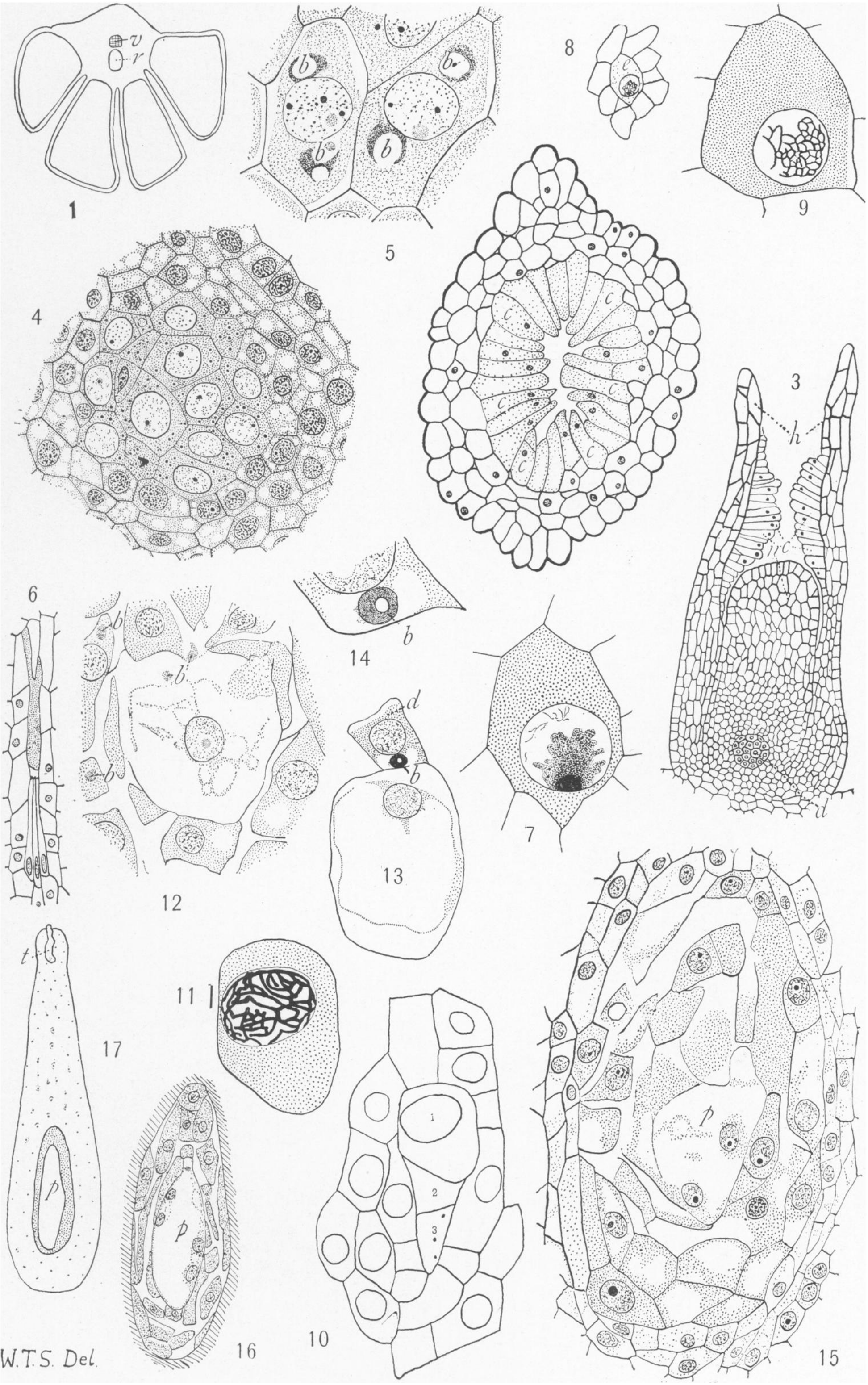
FIG. 44.—Abnormal pollen tube (see text). ×50.

FIGS. 44*a*, *b*.—Nuclei of fig. 44. ×205.

FIG. 45.—Abnormal archegonium. ×205.

FIG. 45*a*.—Part of fig. 45 (see text). ×825.

FIGS. 46*a*, *b*.—Two adjacent sections of the nucleus of an abnormal archegonium. ×825.



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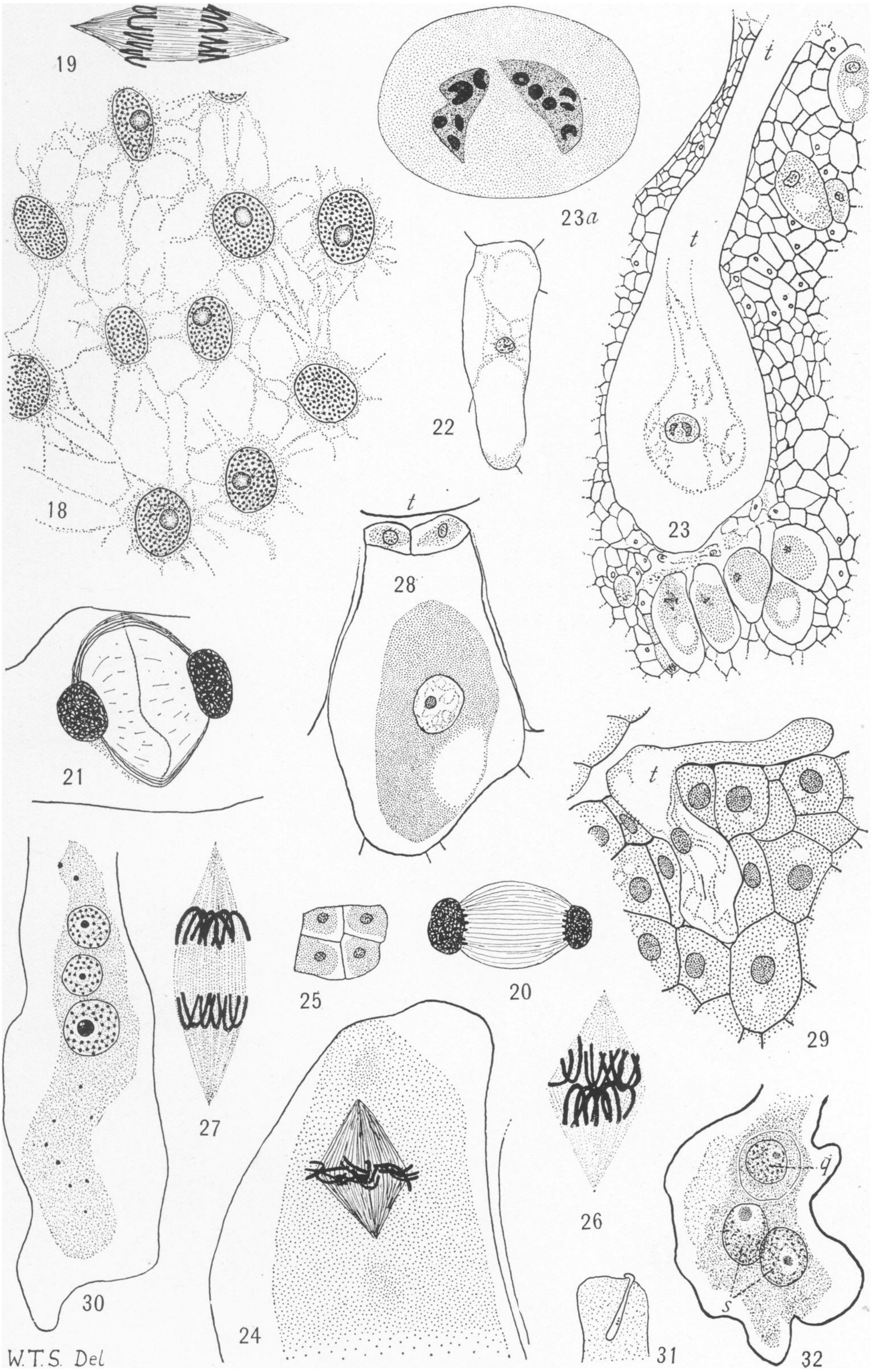

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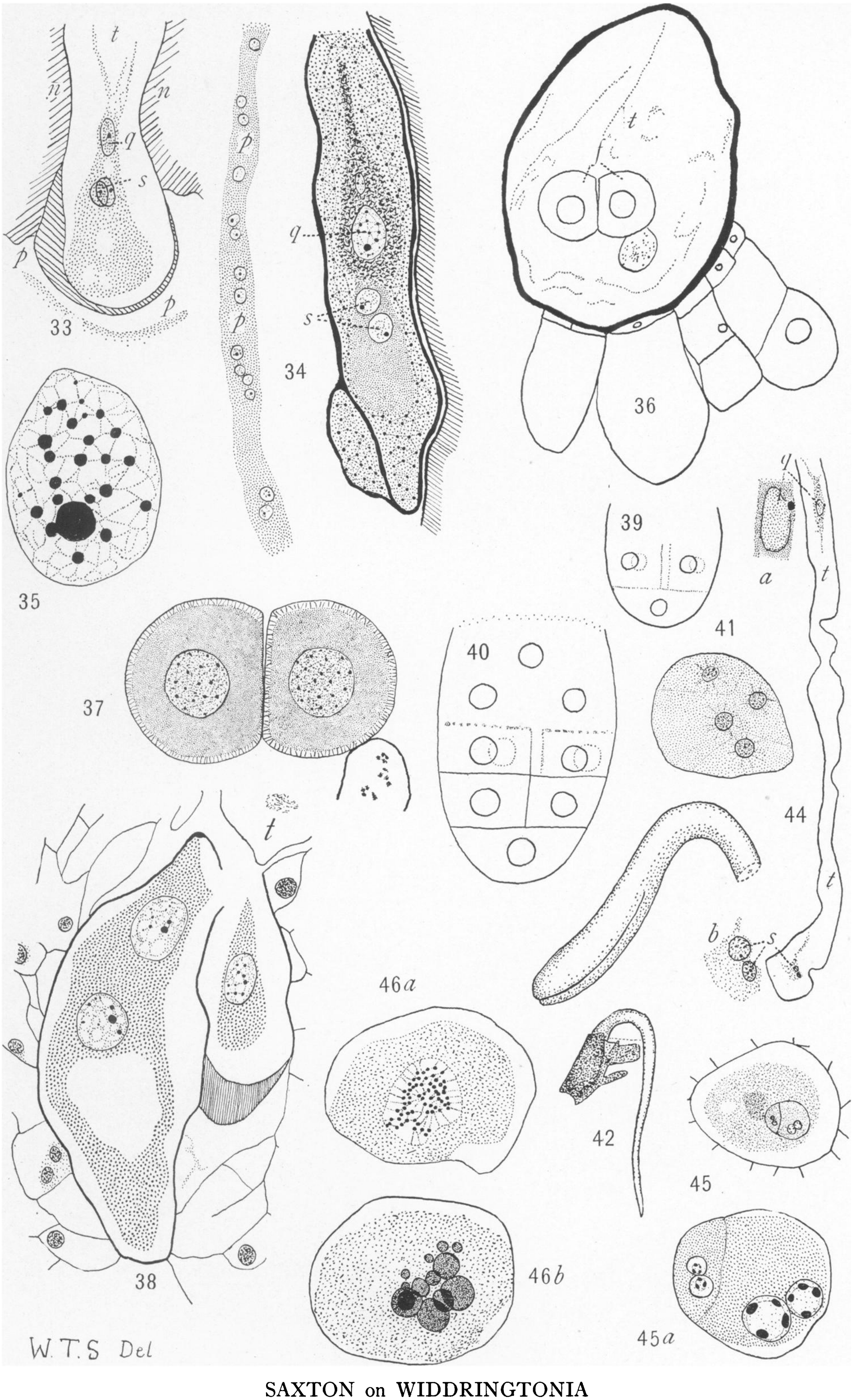

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